# Investigating the Life Position of *Nanogyra Virgula* from the Virgula Marls of the Canton of Jura, Northern Switzerland

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## 1. INTRODUCTION

The Virgula-Marls of the Canton of Jura in northwestern Switzerland are broadly dispersed limestone deposits, famous for trackways of large sauropods (with foot-diameters of more than a meter). This Kimmeridgian formation also records a typical Jurassic marine fauna: crocodiles, fishes, cephalopods and bivalves. The most common organism in the beds is the oyster *Nanogyra virgula* (Defrance, 1820). Though the Marls are widely distributed, there are two different levels with mass accumulations of *N. virgula* (the "Northern" and "Southern" Virgula-Marls).

Until recently, it had been difficult for geologists to date the two Marls, mainly due to the flat plateau morphology (Gygi, 2000); however, quarrying that accompanied the construction of the Transjurane highway provided researchers with sufficient paleontological and stratigraphic information to place the Marls in sequence. The "Northern" Virgula Marls are glauconitic, dark-grey and thin-layered limestone that belong to the uppermost Acanthicum ammonite zone of the Reuchenette Formation in the Upper Kimmeridgian. The "Southern" Virgula-Marls are slightly younger (Jank, *et al.*, 2006).

The Marls are a soft bottom association, but not all layers of the Virgula-Marls are similar. The richest bivalve faunas are found in the bottom layers, but a few layers contain other bivalves, such as *Trigonia*, *Myophorella*, *Goniomya*, *Gervillella*, and *Camptonectes*. It is likely that many other bivalves living in this ecosystem have not been

preserved, since aragonite is completely dissolved in the Marls. At this point, the research on the Marls mainly deals with paleoecological questions. Some of the most intriguing questions pertain to *Nanogyra virgula*, because no conclusion has been made about how these cementing oysters lived.

*Nanogyra virgula* is a small, helicospirally coiled oyster, with a characteristically radial ribbed and convex left-valve, and a flat or slightly concave right-valve (see Figure 1). The attachment scar at the umbonal region is usually very small and involute. The main reason that it is difficult to summarize the life patterns of *N. virgula* is that the majority of shells found are unattached left and right valves. Infaunal bivalves that are found with *N. virgula* are commonly preserved as articulated shells - though they are not necessarily found in life position. However, the thin right valve of *N. virgula* was weakly hinged to the left valve, so when the oyster died, it was very easy for the shells to separate – most likely the presence of a slight current would have detached the valves.

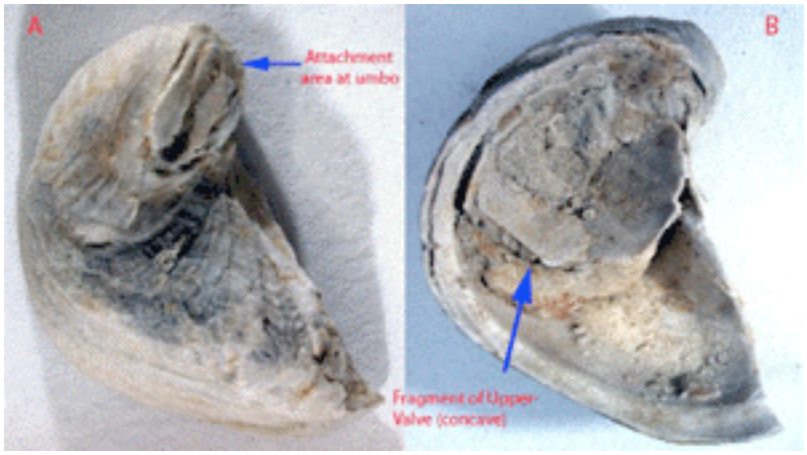


**Figure 1:** The lower valve of *Nanogyra virgula*. The attachment area and umbonal region can be seen in a bottom view (**A**) while the top view (**B**) shows what appears to be fragments of the upper-valve.

*Nanogyra virgula* is very abundant in limestone deposits of southern Germany and northern Switzerland. Scholz *et al.* (2008) reported that Upper Jurassic Nusplingen Lithographic Limestone from Southwest Swabia (Southern Germany) contained very few specimens of *Nanogyra virgula*. It is likely that anoxic conditions found in Nusplingen limestone contributed to the lack of oysters there.

Life positions of fossil oysters and other fossilized, epibenthic bivalved organisms may be reconstructed based on functional morphology and the presence and orientation of epibionts (Seilacher 1984), comparison with recent relatives (Chinzei, *et al.* 1982), and the imprints of substrate in the left and right valves (Machalski, 1989) as well as in the umbonal regions of preserved specimens (Fürsich and Oschmann, 1986 a, b).

The life position of *N. virgula* was discussed by Fürsich and Oschmann (1986 a, b). They argued that in the localities they had investigated, the oysters used other *N. virgula* shells as substrate, and occasionally, infaunal bivalve shells or gastropods. Some of the individuals they investigated showed a smooth attachment area of the umbonal region, suggesting they were the casts of the inner side of infaunal bivalves. Fürsich and Oschmann also concluded that the oysters did not grow on seaweed (as Ziegler, 1969 suggested).

Machalski (1998), studied *N. virgula* fossils from the Marls in Poland, and came to the conclusion that the oyster could have lived in two ways depending on the sedimentation rate: in the case of a soft bottom and a relatively high sedimentation rate, the oyster would have followed a cup-shaped recliner strategy, whereas in the case of a firmer bottom and a lower sedimentation rate, the oyster clustered on conspecifics (forming oyster reefs).

Jens Koppka is one of the researchers currently working in Porrentruy, Switzerland on the vertebrate remains in the "Northern" Virgula-Marls. As a side project, he is interested in the paleoecology of *N. virgula*, because he has found evidence (through shell imprints) that a related oyster, *Nanogyra nana* (found in the older beds of the Banné-Marls), sometimes used the calcareous alga *Goniolina geometrica* as substrate. *N. nana* used nearly the whole valve for attaching to substrate, unlike *N. virgula*, which used only the tip of the shell for attachment. Ziegler's theory of the oysters growing on seaweed should be reinvestigated, because turtles found in the Marls would have spent much of their time in large seaweed beds (if, in fact, their life habits parallel those of living sea turtles).

## 2. Material and Methods of Examination

### 2a. About the Material:

For the present study, I have obtained specimens of *Nanogyra virgula* from Mr. Koppka. There are two batches of oysters, and the batches differ from each other in many ways. The first batch (Batch1) contains approximately 50 oyster valves, all with an average shell length of 1.5 mm. The second batch (Batch2) contains approximately 1000 oyster valves, all with an average shell length of 0.5 mm. Batch1 contains lower valves with a variety of umbonal attachment scars, while the lower valves in Batch2 that remain intact appear to have attachment scars with smooth areas. This suggests life positions on conspecific oysters (an oyster reef). Further descriptions of the examined material are given below.

**2b. Specimen Size:**

The adult shells of most *N. virgula* are about 3 cm (J. Koppka, *pers comm*). The Batch1 material is smaller than this description (average valve size is 1.5 cm) (See Table 1); however, specimens in Batch2 were much smaller than expected (See Figure 2). The average valve size of the oysters in Batch2 was 5 mm (See Table 1). One of larger shells in Batch2 was 9 mm in length. In addition, the examined shells are notably thin and brittle.

**Table 1:** Comparison of Valve size in the Two Batches of *Nanogyra virgula*.

| Batch: | Average Size of Lower (Left) Valve (cm) | Size of Largest Lower (Left) Valve (cm) |
|---|---|---|
| **Batch 1** | 1.5 cm | 2.7 cm |
| **Batch 2** | 0.5 cm | 0.9 cm |

Remarks on Specimen Size:

The observed small shell size in specimens of *N. virgula* from Batch1, and the small shell size and shell thinness from Batch2 is likely the result of taphonomic sorting via disarticulation. In the Batch2, there were a greater number of upper valves than lower valves and very few attached valves (See Section 2d). When the upper and lower valves separate at death, they are sorted by size, weight, and shape. In addition, specimen preparation may cause the shells to become brittle (J. Koppka, *pers comm*).

A second explanation for the small size of *N. virgula* valves is that these specimens lived in a hypoxic (perhaps episodically anaerobic) environment. Most adult bivalves are relatively sessile (aside from protobranchs, pectinids, and a few others, such as *Donax*). They can survive considerable periods of anaerobiosis and can also adapt to live continuously under hypoxic conditions. One adaptation to low oxygen supply is the ability of bivalves to couple anaerobic respiration with a drastic reduction in energy demand (Vakily, 1992). Smaller body size is more energy effective, and Dame (1996)

suggests a power law for the relationship between oxygen consumption and bivalve size (smaller body sizes occur during periods of anaerobic/hypoxic conditions). Differences in shell length are coupled with changes in organic content of the larvae, and a reduction in shell growth reflects a decrease in tissue growth under hypoxic conditions.

Wang and Widdows (1991) reported that hypoxic environmental conditions do not discourage larval settlement in the mussel *Mytilus edulis* (water movement was the overriding stimulus), but low levels of oxygen resulted in increased erosion of the prodissoconchs and a decreased rate of shell secretion. Extended anoxia kills economically important oysters today (Baird, *et al.* 2004), and it is doubtful that any bivalves can survive anaerobic conditions indefinitely. In the case of *N. virgula* exposure to reduced oxygen levels during development might account for the atypical size and shell thickness; however, the disarticulation of valves indicates that there was quick degradation of the adductor muscle, which is characteristic of aerobic conditions upon burial.

Scholz *et al.* (2008) reported that Upper Jurassic Nusplingen Lithographic Limestone from southwest Swabia (southern Germany) contained very few specimens of *Nanogyra virgula*. Undisturbed lamination in the sediments of this deposit strongly points to oxygen-free conditions on the seafloor and within the sediment. The few specimens of *N. virgula* that the researchers reported were quite large, and likely drifted in on an ammonite shell. Since *N. virgula* is abundant in limestone deposits of higher energy, the rarity of *N. virgula* in Nusplingen may be a result of the hypoxic to anaerobic conditions in the living environment.

## 2c. Shell Morphology:

The shapes of the upper and lower valves from Batch2 were analyzed (See Figure 2). These specimens appear to have little variation in shell shape. The upper valves are generally flat and slightly concave, and the lower valves appear as convex, cup-shaped shells. In living position, the oyster shell would have curved to the right. Within the sample of lower valves, some of the valves appeared to have a rapid expansion of the curvature towards the posterior end of the valve, while other valves appeared to have a more constant exponential growth. Batch1 mainly consists of lower valves, which vary slightly in degree of shell curvature.

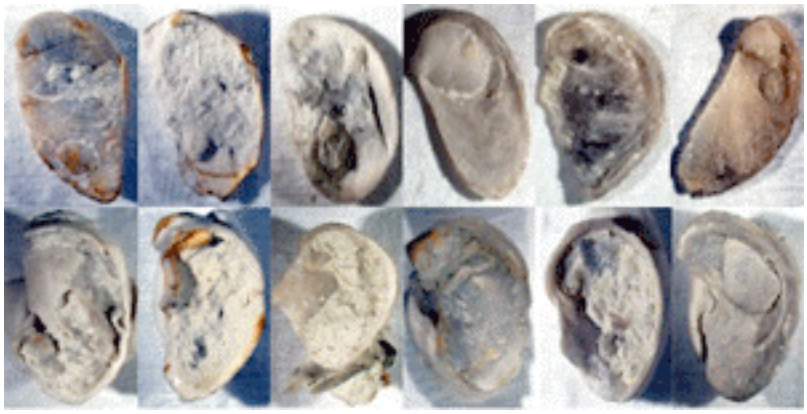

**Figure 2:** Detached Valves of *Nanogyra virgula* from Batch2. Shell morphology is curved. (**Top**) Top of upper (right) valves (**Bottom**) Bottom of lower (left) valves.

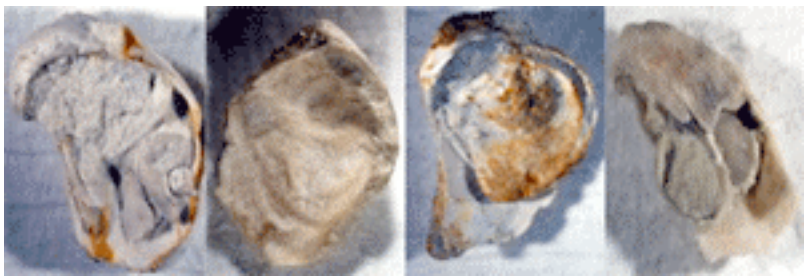

**Figure 3:** Examples of Attached Valves of *Nanogyra virgula* from Batch2.

Remarks on Shell Morphology:

The generating curve of a shell can expand slowly or quickly. Most bivalves expand their shell circumference very quickly, giving the typical shallow-bowl morphology (scaphopods, which have two centers of calcification lateral to the apical slit, expand very slowly, giving a narrow cylinder). Shell geometry is developmentally constrained, because the two valves must fit together at all times, so there is a limit on the range of forms that they take on. Because the shell cannot be resorbed, the two valves cannot be remodeled and must always fit together. The umbonal region is predisposed to cause difficulties (if the umbos were to touch, the ligament might be prevented from opening the valves). In some cases, bivalves have found ways to defy developmental restrictions on shell growth. For example, some bivalves crack their ligaments in order to secrete new shell material, and they subsequently reinforce the hinge from within (Seilacher, 1984).

Generally, the two valves are mirror images, though there are many exceptions. In the case of reclining oysters, the two valves fit together, but otherwise show different degrees of curve expansion (the lower valve forms a "lip" at the edge of the upper valve, and this restricts the upper valve's growth). Lip forming is another common solution in bivalves to the constraints on shell morphology (Seilacher, 1984). The "gyra" in *Nanogyra* describes the rapidly increasing distance of the generating curve from the axis of coiling that is seen in the lower (left) valve. At the same time, the complementary upper valve is nearly flat (a result of rapid expansion and little translation down the axis of coiling).

The ability of mantle to attach shell to a hard substrate does not extend beyond very small, newly settled individuals (the foot and byssus are central in initiating

attachment). In the case of *Nanogyra virgula*, the oyster attached to other shells at settlement, but as an adult, it probably rested on unconsolidated substrate – with the lower (left) valve serving as an anchor.

**2d. Valve Bias and Shell Orientation:**

In Batch1, the majority of shells were lower (left) valves (about 75 %). In addition, a number of valves from Batch1 attach to the bottom of a conspecific's lower valve. The valves in Batch2 were mostly upper valves. Out of 304 examined specimens, 227 (75%) were upper (right) valves, 54 (17%) were lower (left) valves, 6 (2%) were attached valves, and 17 (6%) were unidentifiable material (See Table 2).

**Table 2:** Number of Lower, Upper, and Attached Valves in 304 *N. virgula* shells from Batch2.

| Number of Lower (Left) Valves | Number of Upper (Right) Valves | Number of Attached Valves | Number of Unknowns | Total Number of Specimens Examined |
|---|---|---|---|---|
| 54 | 227 | 6 | 17 | 304 |

Remarks on Valve Bias and Shell Orientation:

Some of the difference between the two batches can be attributed to sampling bias. It is unclear whether the collector of Batch1 handpicked lower valves in the hope of acquiring specific information about larval development and oyster life positions. Batch2 is more comprehensive in regard to shell shape and size; however, Batch2 contains only specimens of *N. virgula*, whereas the Batch1 includes other mollusks that were preserved in that habitat.

As mentioned earlier, the apparent valve sorting (a majority of upper (right) valves) in Batch2 can be attributed to taphonomic disarticulation. Disarticulation of bivalve shells occurs very rapidly after death - without muscular opposition, the ligament splays the valves open. In fact, because bivalves have the ability to escape sediment

burial, the rare occurrence of many articulated or closed bivalve shells indicates death within burrows or rapid and heavy substrate burial (Brett and Baird, 1986).

One adaptation to living on the soft bottom of the sea floor is a recliner position. In this scenario, bivalves will orient on their side, with a deep, convex valve that anchors the animal in the sediment. The other valve will be slightly concave or flat and rest on the deeper valve, at or just below the interface of sediment with the water column. The functional difference between the valves in this case is superimposed on the valves' chiral symmetry (Seilacher, 1984). Either valve can be the cup that holds the body – the left valve in *Chama*, but the right valve in *Pseudochama* (though, *Pseudochama inezae* has been found to attach indiscriminately by either valve - Campbell, *et al.* 2004).

The finding in Batch1 that many young oysters attach to the bottom of a conspecific's lower valve suggests that they were settling on overturned, dead valves. The recliner life form typically inhabits environments that were relatively quiet, with a deep enough water column to escape being overturned by storms. The rare storms that did reach these environments probably account for their preservation in the fossil record. In such cases, evidence of abrasion and rolling is often found.

**2e. Type of Preservation:**

The valves from both batches appear to be body fossils (I placed a valve into HCL, and it fizzed and bubbled). In addition, the unidentified bivalve (likely *Trigonia*) from Batch1 appears to be a steinkern (See Figure 7 - for the moment, I do not have a macro image of this bivalve specimen).

Remarks on Type of Preservation:

Within fossil assemblages, differential preservation of various taxa may reflect original mineralogy. I conclude that the *N. virgula* material I have contains body fossils,

because the original calcite fizzed when tested with Hydrochloric Acid (HCl). Calcite is the predominant mineral in oyster shells, and it effervesces carbon dioxide when exposed to acid. Prolonged exposure or reworking in normal marine environments will degrade aragonitic shells before calcitic shells. Because of this, calcitic shells are commonly preserved as robust, minimally altered fossils, in the same sediments where aragonitic shells are dissolved or preserved as highly deformed, composite molds.

Although most burrowing bivalves are aragonitic, epibenthic bivalves are usually partially or entirely calcitic (Checa *et al.* 2007). In some regimes, this difference might mean that the infaunal clams would be forgotten upon fossilization, leaving entirely epibenthic fauna to guide the fossil record. On the other hand, Lazo (2004) found that a species (*Protothaca staminea*), which can be found infaunally and epifaunally (on gravel), showed considerably more damage in the latter environment when exposed to chemical and physical factors. He suggested, therefore, that infaunal bivalves are more likely to fossilize. However, the difference between aragonite and calcite is a more important factor to consider in paleoecological reconstruction.

**2f. Methods of Examination:**

Measurements of specimen body parts were obtained with the image analysis program, *Image J.* Valve length was measured from the base of the umbonal region to the posterior edge of the shell.

A stereomicroscope and a macro-lens camera were used to digitally image the specimens. The best angle of light projection was at the side of the specimen, parallel to the stage, or directly above the specimen. Images captured were high quality to maintain resolution. Lighting and contrast were adjusted on some images with Adobe Photoshop – no other alterations were made.

Some specimens were used for anatomical studies, which included high-vacuum Scanning Electron Microscopy (SEM) imaging. In this case, no chemical preparation was needed, because the shells were already dry. Sputter-coating was performed for high-vacuum observation (coating time of 120 to 150 seconds). The samples were mounted on aluminum SEM pins with carbon glue. A strip of silver was applied to larger specimens (in order to decrease potential electron charging).

In addition to microscopic observation, some specimens were observed under a Camera Lucida. This technique allowed for the duplication of some key points in the specimens, and was useful in providing a more accurate perspective of the fossils

## 3. Attachment Area and Umbonal Impressions

Bivalves feed and disperse as veliger larvae in the plankton. When they are small in size (and easily carried away by currents), the bivalve needs to stabilize by attaching to substrate. They use chemical and physical cues to choose the appropriate substrate (hard or soft) on which they settle. Bivalves generally use a byssus to anchor themselves to hard substrates, or tether themselves to soft ones. Upon settling out of the plankton, an oyster crawls around on its foot, investigating potential substrates. It then empties its large byssal gland between one valve and the substrate that it has chosen (Nelson, 1924). Subsequently, some species, including *Crassostrea*, use the shell material secreted by the mantle to extend the area of attachment.

The material onto which the larva attaches will often be impressed into the umbonal region of the shell. In the case of oysters, the umbo of the lower valve will often carry the impression because the organism lives sideways. Oysters are known to attach themselves, initially, to many different types of substrate for stability including seaweed,

other bivalve shells, gastropods, driftwood, rocks, and in the Mesozoic, ammonites. When trying to figure out the paleoecology of a fossil bed, umbonal regions of bivalves can often indicate other substrates and organisms present during the time period.

I examined the umbonal regions of specimens from both batches. The majority of the specimens showed smooth attachment areas. In a few specimens, there are different structures. A pictorial analysis of different umbonal imprints is give below.

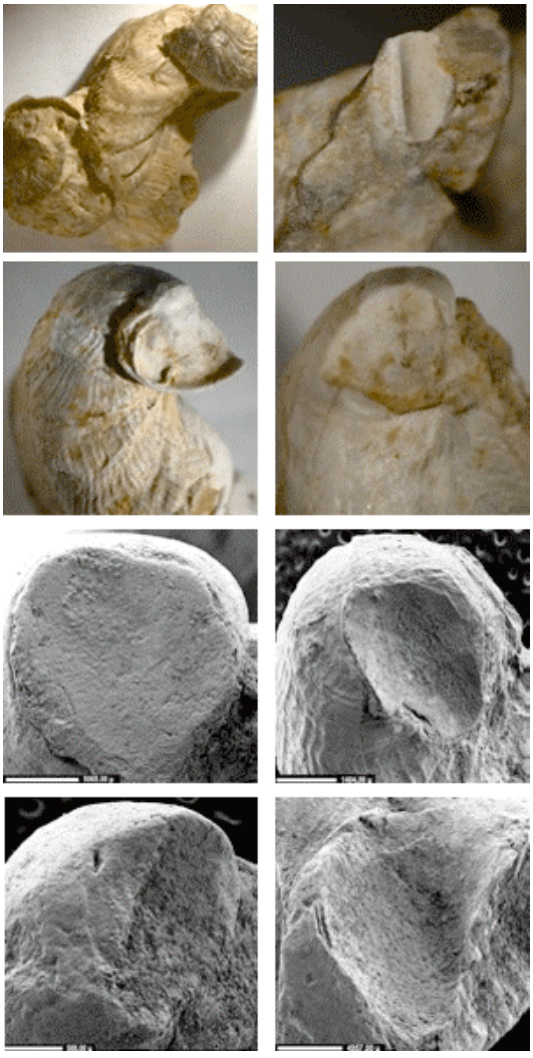

**Figure 4:** Umbonal region of specimens *Nanogyra virgula* from Batch1. These specimens attached to other *N. virgula* as larvae. (**Top 4 Images**) Valves show smooth attachment area, or the presence of other *N. virgula* valves in the umbonal region (top left image is an apparent oyster colony). (**Bottom 4 Images**) SEM images of smooth attachment areas.

**Figure 5:** Oyster attachment scars on specimens *Nanogyra virgula* from Batch1. These specimens show scars from other attaching *N. virgula*. (**Top Image**) Bottom of lower (left) valve shows multiple scars (was specimen overturned and dead when scars were made?) (**Middle Image**) Top of upper (right) valve (specimen with valves attached) that shows scars from other oyster attachments. (**Bottom Image**) Examples of scars of oyster attachments on valves of various specimens of *Nanogyra virgula* in Batch1 (scars range from 1.5 to 5 mm in length).

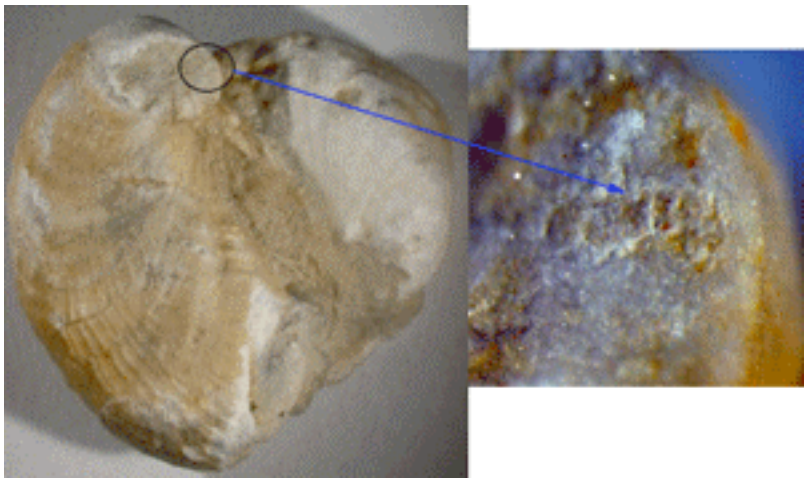

**Figure 6:** Umbonal region showing attachment scar to an apparent certhiid gastropod. (**Left Image**) Bottom view of lower (left) valve. (**Right Image**) Close up of attachment scar (scar is approximately 1 mm in length – specimen is approximately 1.3 cm in length.

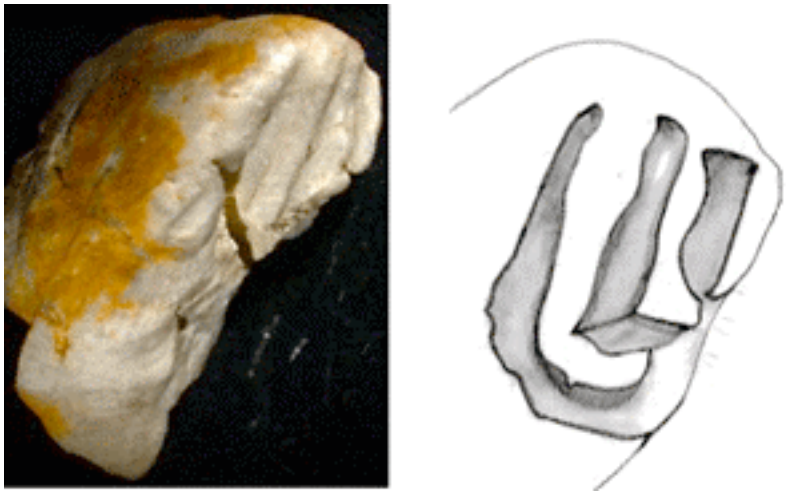

**Figure 7:** Umbonal region of oyster specimen shows unique attachment scar (what appear to be three "prongs"). (**Left Image**) Bottom view of lower (left) valve (umbonal region is in the upper left corner of the picture). (**Right Image**) Camera Lucida drawing of umbonal region – this picture is not particularly accurate but shows an apparent "branching" of the three prongs. In the future, I would like to take an SEM image of a cast of this area.

**Figure 8:** Ideas about the substrate that the valve in **Figure 7** attached to. (**Left Image**) Steinkern of an apparent trigonid bivalve that was collected along with the Batch1 material. The ridges appear similar in shape to the umbonal scar. (**Right Image**) Example of an ammonite shell (*Aulacostephanus pseudomutabilis* , Lower Kimmeridge Clay) with tri-branching septa. This is another possible substrate; however it is unclear if ammonites have been found in the material. (Right Image copyright Ian West, 2009)

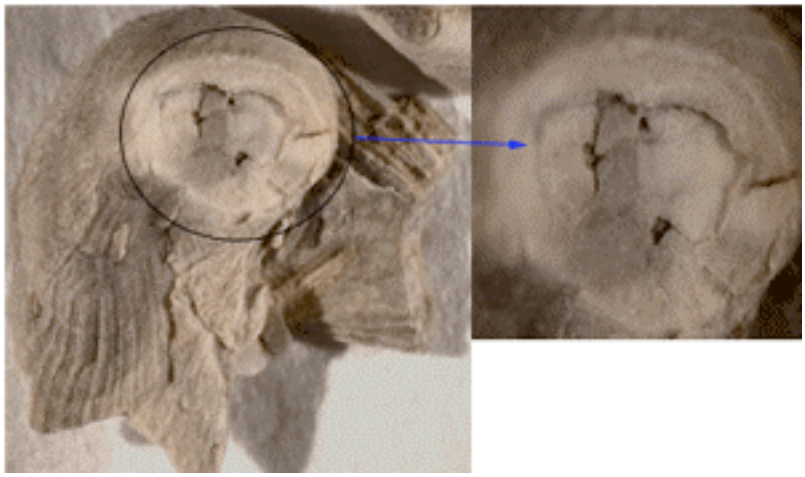

**Figure 9:** Umbonal region showing attachment scar to an apparent procerithiid gastropod. (**Left Image**) Bottom view of lower (left) valve. (**Right Image**) Close up of attachment scar (scar is approximately 8 mm in length – specimen is approximately 1.5 cm in length)

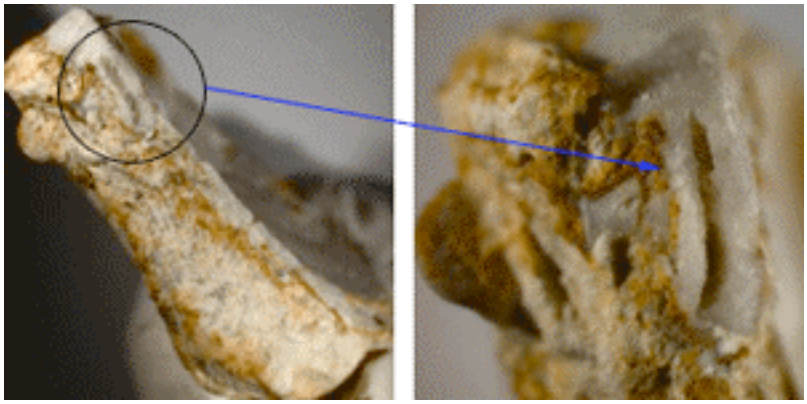

**Figure 10:** Umbonal region showing attachment scar to an unknown object. (**Left Image**) Side view of lower (left) valve. (**Right Image**) Close up of attachment scar – this oyster possibly attached to the edge of another *N. virgula* valve, though such a selection on the oyster's part would not have been very wise (scar is approximately 8 mm in length – specimen is approximately 2.0 cm in length).

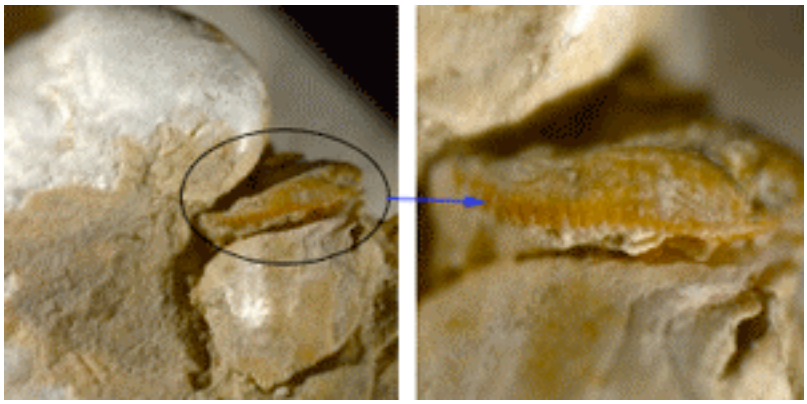

**Figure 11:** Strange fossil found with oyster colony. (**Left Image**) Bottom view of lower (left) valve with strange specimen to the right. (**Right Image**) Close up of strange fossil (specimen is approximately 8 mm in length – oyster is approximately 1.7 cm in length)

**Figure 12:** Strange fossil found with oyster colony (specimen is approximately 1.2 cm in length)

**Figure 13:** The bottom-view of a lower valve of *Nanogyra virgula*. What appear to be bryozoan borings are seen imprinted on the shell surface.

## 4. DISCUSSION

While investigations in taphonomy provide valuable information on biogeological details and modes of life, arriving at conclusions about fossils, which have missing characters or deformed features is not an easy task. In this way, it is important to find answers through links in other systems. I have looked at the shells and observed many interesting things that can yield a bigger picture about the life of the oysters. There are still holes that will not be filled in this time, but I am confident that some of the conclusions I have made suggest ideas about the oyster and its life habits.

The life position of *Nanogyra virgula* specimens varies within the samples that I have been given. I have found the shells attached to other specimens of *N. virgula*, other bivalves, and gastropods. This suggests that the larval oysters need to stabilize on hard substrate so that they do not become buried in the mud. The specimens that attach in colonies and form "oyster reefs" were probably at an advantage because they had more potential for finding food resources, and potential mates also surrounded them. Under this reasoning, the fact that some oysters were attaching to the bottom of lower (dead) valves seems unwise; however it may have been that overturned lower valves provided better anchors for the young oysters than did thin, easily unhinged upper valves.

The presence of algal/fungal microborings in shells from the early Paleozoic onward not only provides an important indicator of shallow, photic-zone environments, but also may be a sensitive gauge of relative exposure times on the sea floor. The suggestion of algal borings is intriguing, but I have not found any evidence for this in these specimens. I believe that I have evidence of bryozoan epibionts on one shell (See Figure 13). An interesting note is the absence of boring sponges on any of the shells.

Perhaps this is a line of evidence for a low oxygen environment. Sponge feeding is based on uncoordinated beating of choanocyte flagella, which requires a lot of oxygen, so sponges are not creatures in hypoxic environments.

This study is incomplete as it stands. There are more opportunities for investigations of umbonal regions, and more information to obtain from the different fauna collected with *N. gyra*. A much larger, unbiased sample from environments that could be characterized on the basis of features other than the morphology of *Nanogyra virgula* could give insight into paleoecology of the deposit. In addition, an appropriate model of shell growth in *N. virgula* might account for the range of forms observed.

The interesting direction to go in from this study would be an investigation on the impact of substrate attachment and morphology of the oyster. Do differences in substrate attachment affect the subsequent shape of the valves? Could the effect of this initial state be teased apart from environmental differences that correlate with substrate availability? Developmental and environmental constraints channel the phenotype at the epigenetic level. Meanwhile, at the underlying genomic level, accumulated alleles will sort out best outcomes. This selection for the most functionally useful genes is omnipotent and likely aligned with architectural constraints, so we can probably ignore it. Considerations should turn to how the whole organism stays in tune with its environment. Such investigations lead to discussions of fabrication, functional anatomy, and the meeting with the effective environment – that is evolution.

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